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Observations on the Bionomics of the Bee *Andrena (Tylandrena) erythrogaster* Ashmead (Hymenoptera: Andrenidae)

with notes on *A. (Micrandrena) personata* Robertson and *A. (Holandrena) c. cressonii* Robertson

Eugene R. Miliczky

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Pictured on the cover is *Andrena (Tylandrena) erythrogaster* Ashmead visiting *Salix discolor*. Photo by Michael Jeffords of the Illinois Natural History Survey.

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Illinois Natural History Survey
Natural Resources Building
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Observations on the Bionomics of the Bee *Andrena* (*Tylandrena*) *erythrogaster* Ashmead (Hymenoptera: Andrenidae)

with Notes on *A.* (*Micrandrena*) *personata* Robertson and *A.* (*Holandrena*) c. *cressonii* Robertson

Eugene R. Miliczky

The bee genus *Andrena* is Holarctic in distribution with about 500 species inhabiting North America and perhaps 700 species in Eurasia (LaBerge 1986b). Several species can often be found in local parks and preserves and in other small areas of undisturbed habitat that provide nesting and foraging opportunities. Intensive collecting at one such site in the present study (Homer Lake, 288 ha) yielded 42 species from late April to the end of June (Miliczky 1985). At another site (Lodge Park, 83.4 ha), 24 species were collected during the same period (Miliczky personal observation). *Andrena* not uncommonly nest in lawns and yards, forming aggregations of dozens or hundreds of individuals (Stephen 1966; Johnson 1981; Miliczky personal observation). Recent papers (Davis and LaBerge 1975; Schrader and LaBerge 1978; Barrows 1978; Norden and Scarbrough 1979; Johnson 1981, 1984; Parker and Bohart 1982; and Parker and Griswold 1982) provide behavioral and ecological data on North American species. In the mid-fifties, Michener and Rettenmeyer (1956) summarized the information known to them concerning Old World *Andrena* biology. Since then, papers on the biology of Old World *Andrena* include Hirashima (1962), four species from Japan; Wafa, Rashad, and Moustafa (1972) and Rashad and Moustafa (1973), *A. ovatula* (K.) in Egypt; and Radchenko (1981) and Popova (1983), four and six species, respectively, from the Soviet Union. Nevertheless, information concerning nesting, reproductive, foraging, and other behaviors is limited to a small percentage of the species, and entire subgenera remain unstudied.

The purpose of this paper is to present information on the nesting biology of *Andrena* (*Tylandrena*) *erythrogaster* Ashmead. During a study of *Salix*-visiting bees (Miliczky 1985), nests of this species were found at two locations in east-central Illinois and were observed during the 1981–1984 seasons. Several nests of *A.* (*Micrandrena*) *personata* Robertson and one of *A.* (*Holandrena*) *cressonii cressonii* Robertson were found as well, and limited observations of these two species are included.

Andrena erythrogaster (Figure 1), the most abundant member of its subgenus, ranges from Maine to British Columbia and from southernmost Canada to northern New Mexico, Oklahoma, and Georgia. In the western United States it is replaced by the closely related *A. subaustralis* Cockerell. The species is an oligolege of willows (*Salix* spp.) and has been collected mainly during April and May (LaBerge and Bouseman 1970). Rau (1935) called it the red-bellied bee because of its frequently red or partially red abdomen and has provided the only other behavioral observations of the species.

Materials and Methods

Each nest under observation was marked with a small nail placed adjacent to the entrance. A common reference number was assigned to each nest and its adult female, but the bees themselves were not marked. Observations at nesting sites were recorded with a portable cassette player and transcribed in the laboratory. Events were timed to the nearest half-minute during 1981 and 1982. A digital watch was used in 1983, and events were timed to the nearest second. Times were in central daylight-savings time. Air temperature was taken periodically during the day with a thermometer hung 1–2 m above ground in a shaded location. General weather conditions were also noted at these times, especially cloud or wind conditions that might affect bee activity.

Nests were excavated with an assortment of knives and trowels by carefully following the main burrow from soil surface to cell depth. Well-compacted soils made filling main burrows with plaster of paris unnecessary. A pair of small dissecting scissors was used to cut small roots without unduly disturbing the soil near exposed cells. Larger roots were severed with wire cutters. Artist's brushes moistened with water were useful for removing debris that inevitably fell into exposed cells. The soil surrounding exposed cells was carefully moistened with water from an eyedropper to stabilize it and to reduce contamination of cell contents. Exposed cells were covered with pieces of

Dr. Miliczky is a former research assistant with the Section of Faunistics and Insect Identification at the Illinois Natural History Survey. This paper is part of his Ph.D. dissertation in entomology completed at the University of Illinois at Urbana-Champaign in 1985.

moistened paper or cardboard to keep out debris. A rough sketch of each nest as seen from above was made in the field to record the orientation of each cell with respect to the main burrow.

During 1981, several large blocks of soil containing entire nests were brought into the laboratory for careful excavation. In subsequent years, as familiarity with nest structure increased, most excavation was done in the field, and only small blocks of soil that contained single cells were retained. Even then, however, larger blocks of soil were removed when cells were close together or time did not permit careful excavation in the field.

Attempts to rear immatures were moderately successful. A number of postdefecating larvae were transferred to cell-shaped depressions in wax-filled petri dishes. Feeding larvae were left in their natal cells and placed in soil-lined plastic containers with tight-fitting lids. The soil was kept moist and the cells were checked regularly for mold.

FIGURE 1. Female *Andrena erythrogaster* foraging on a male catkin of *Salix interior*, Homer Lake, 7 June 1983.

Data on adult flight periods for 1983 and 1984 were obtained from extensive collections of bees visiting four species of *Salix* on fair weather days at the Homer Lake site. Collections were made at hourly intervals between 0800 and 1800. The time of the first collection and the number of subsequent collections on a given day depended on weather conditions because temperature and cloud cover influenced the onset and level of bee activity. Bees taken in a collection were cooled in an ice chest to induce a temporary state of torpor. This practice allowed many specimens to be identified in the field and returned, unharmed, to the population. The vast majority of *Andrena erythrogaster* were so returned.

All photographs were taken by the author with a Nikon FM2 camera and 50 mm lens. The camera was fitted with flash and Vivitar extension tubes for macrophotography. Measurements and drawings of cells were made with the aid of an M5 Wild stereomicroscope equipped with an ocular micrometer and drawing attachment.

Specimens of adult and immature stages and samples of nest structures taken during this study were deposited in the insect collection at the Illinois Natural History Survey in Champaign, Illinois.

Description of Nesting Sites

Nests of *Andrena erythrogaster* were discovered at two sites within the Piatt County Forest Preserve (henceforth referred to as Lodge Park) on 25 April 1981. Lodge Park lies 3.2 km north of Monticello, Illinois. The Sangamon River meanders through it, and its natural vegetation is wet, mesic, floodplain forest.

The first site was a narrow grassy area, 5–7 m wide and 70–80 m long, between the park road and a small pine plantation. The site ran north-south, sloped gently to the east, and received sun for much of the day. A strip 1–2 m wide of mostly bare soil ran through the middle of the grassy area, and two nests of *Andrena erythrogaster* were found near the south end of this strip. Deep tire ruts were present, and the strip appeared to have been scraped of vegetation by a vehicle. The nearest willows were about 100 m away. About 15 *A.* (*Melandrena*) *barbara* Bouseman and LaBerge also nested in the bare strip or in the short grass on either side, and several nests of unidentified bees and wasps were in the area as well. When the site was revisited in August, a small aggregation of a species of *Cerceris* (Hymenoptera: Sphecidae) was using it. A few preliminary observations of *Andrena erythrogaster* were made at this site.

The second and principal Lodge Park nesting site was in the wooded, northern section of the park along a narrow, little-used footpath 25–30 m from the park road. All nests were in level ground within 2 m of the northern edge of the footpath. Seven or 8 m north

of the path, the ground dropped abruptly (2–3 m) to the Sangamon River floodplain. In late April, the forest canopy was largely open, and new herbaceous growth on the forest floor was sparse. Organic debris (leaves and twigs) was scattered on the ground, but bare and moss-covered areas were present as well. As the season progressed, the canopy filled in and vegetation on the forest floor became more dense. Fourteen *Andrena erythrogaster* nests were found within an area measuring about 2 × 4 m; nine of these were observed during the 1981 season. Three other nests were found a few meters west of the main group, and other individuals probably nested elsewhere along the path. The nearest willows were 175–200 m from this nesting site. Numerous species of spring wildflowers bloomed in the surrounding woods and provided pollen and nectar for the many species of wild bees that occurred in the area. Among the most abundant were *Claytonia virginica* (Portulacaceae) and *Dentaria laciniata* (Cruciferae), both of which were visited by wild bees.

Nests of other native bees in the main area included many nests of *Andrena personata*, which began to nest about mid-May; two nests of *A.* (*Euandrena*) *geranii* Robertson, which was quite abundant and visits *Hydrophyllum* spp. (LaBerge 1977); one nest of *A.* (*Ptilandrena*) *erigeniae* Robertson, an oligolege of *Claytonia* (Davis and LaBerge 1975); three nests of a large species, perhaps *A.* (*Melandrena*) *illini* Bouseman and LaBerge or *A.* (*M.*) *pruni* Robertson, both of which were collected in the immediate vicinity; three nests of unidentified *Andrena*; one nest of a *Dialictus* sp. and one of an augochlorine bee.

I returned to this site in 1982 and discovered two *Andrena erythrogaster* and several *A. personata* nests during observations from 13–17 May.

Another location at which nests of *Andrena erythrogaster* were found was the Salt Fork River Forest Preserve (henceforth referred to as Homer Lake), 3.2 km NW of Homer, Champaign County, Illinois. The Salt Fork River forms the southeastern boundary of the preserve, and the nesting site was located on its floodplain, about 200 m north of the river, just south of the Homer Lake dam. Nests were discovered about 17 May 1983 in an area of a meadow where the vegetation had been well trampled by my own activities. The trampled area was on level ground and measured about 4 × 5 m. Ten *A. erythrogaster* nests and one *A. cressonii* nest were found within or slightly outside of the area. Vegetation in the meadow was predominantly grasses, but many young *Solidago* plants were scattered throughout along with a few *Zizia aurea* plants, a patch of poison ivy (*Rhus radicans*), and several small saplings. A willow thicket with four species of *Salix* (*S. amygdaloides, S. interior, S. nigra,* and *S. rigida*) was less than 30 m west of the nesting site. Some large trees 25 m to the east shaded the nests during the early morning. Many flowering plants, in addition to the willows, provided pollen and nectar for the numerous species of wild bees at Homer Lake. Among the most abundant of those that bloomed during the study were *Prunus virginiana* and *Rubus* spp. (Rosaceae) and *Zizia aurea* (Umbelliferae).

Active Seasons of Adults

Extensive collections of *Andrena erythrogaster* (and other bees) visiting the four species of *Salix* at Homer Lake during 1983 and 1984 give an indication of the active season of the adult bees, and this information is shown in Figure 2. The flowering seasons of the four species of *Salix* found at the site are also shown because *Salix* spp. are the principal pollen sources of the oligolectic *Andrena erythrogaster*.

Collections were made on 19 days during 1983, the first on 27 April and the last on 22 June. A total of 297 females was taken, the first 3 on 27 April. The number of females taken in collections increased during early May, leveled off and remained steady through the first week of June, and decreased after 8 June. The last 5 specimens were taken on 17 June. Males were abundant on the first day of collecting, when 18 were taken, but decreased in number thereafter. None was taken on the eight collecting days that fell after 17 May and before 17 June, as shown in Figure 2; however, on the last two collecting days, 17 and 22 June, 2 well-worn specimens were netted each day. A total of 59 males was taken.

Sampling during 1984 was more intensive and yielded 2,448 females and 183 males in 33 days of collecting from 25 April through 29 June. Seasonal distribution of females was similar to that of 1983. No bees were taken on 25 or 26 April, but a single specimen was netted on the 27th. Numbers increased rapidly during early May and began to decline after 1 June. Three worn bees were taken on 15 June, but none was netted on the last four collecting days. Seasonal distribution of males in 1984 was similar to that of the previous year. A single bee was netted on 25 April, but numbers increased thereafter, reaching a peak (40 bees) on 1 May and then steadily decreasing. The last specimen was taken on 17 May. *Andrena erythrogaster* has a single generation per year.

Collections from host plants indicated a minimum period of activity for females of 52 days during 1983 (27 April–17 June). Similarly, females were active for at least 50 days during 1984 (27 April–15 June). Some idea of the flight period of individual females was obtained during the 1981 observations, which spanned much of the active season of the species. Observations began on 26 April, when nesting was underway, and ended on 1 June, after which nest excavations began. One bee survived this entire period and was seen by chance still provisioning her nest on 4 June. She had been active for at least 40 days. Another bee had been active at least 33 days, based on the final

day of observation. Three individuals, on the other hand, were active for fewer than 10 days each. One was found dead in her nest, and the fate of the other two is unknown.

In contrast to females, males were active at the willows for a much shorter period. They appeared on host plants a day or two before the females, rapidly increased in numbers, and then showed a steady decline. During 1983, the principal period of male activity extended from 27 April to 17 May (21 days). Some males survived beyond this time, as evidenced by specimens captured on 17 and 22 June. Most, however, had disappeared by mid-May. The period of male activity during 1984 was at least 22 days (25 April–16 May).

Although mating was not observed, sexual activity may occur at host plants because males frequently visit willows for nectar and encounters between the sexes are likely. Mating occurs at the host plant in certain other *Andrena*. For example, a pair of *A.* (*Micrandrena*) *nigrae* Robertson was taken *in copulo* on *Salix interior* on 20 May 1982, and I have observed male *A.* (*Trachandrena*) *mariae* Robertson patrolling willows and pouncing on foraging females. Both species are *Salix* oligoleges. Mating in the polylectic *Andrena cressonii* occurs on host plants (see below), and Linsley and MacSwain (1959) reported that *A.* (*Euandrena*) *caerulea* Smith (= *complexa*) and *A.* (*E.*) *suavis* Timberlake mate on the flowers of their host plant, *Ranunculus californicus*. Other activity among male *Andrena erythrogaster* includes patrolling nonhost plants (maples, for example) as I observed during 1982. Rau (1935) reported that males flew about the nesting site and entered the burrows of nesting females on occasion. No male activity was observed at nesting sites during the present study, however.

Nest and Cell Structure

Bees dug their nests in locations that provided various degrees of concealment and protection from wind and rain. The two nests found at the roadside site in Lodge Park were in bare soil, exposed and unprotected. After the tumuli had been blown or washed away, however, the entrances were not obvious. Six nests in the wooded site at Lodge Park had entrances partly or completely surrounded by moss, but seven others were in areas of bare soil. Entrances to these 13 nests were ill-concealed, although those

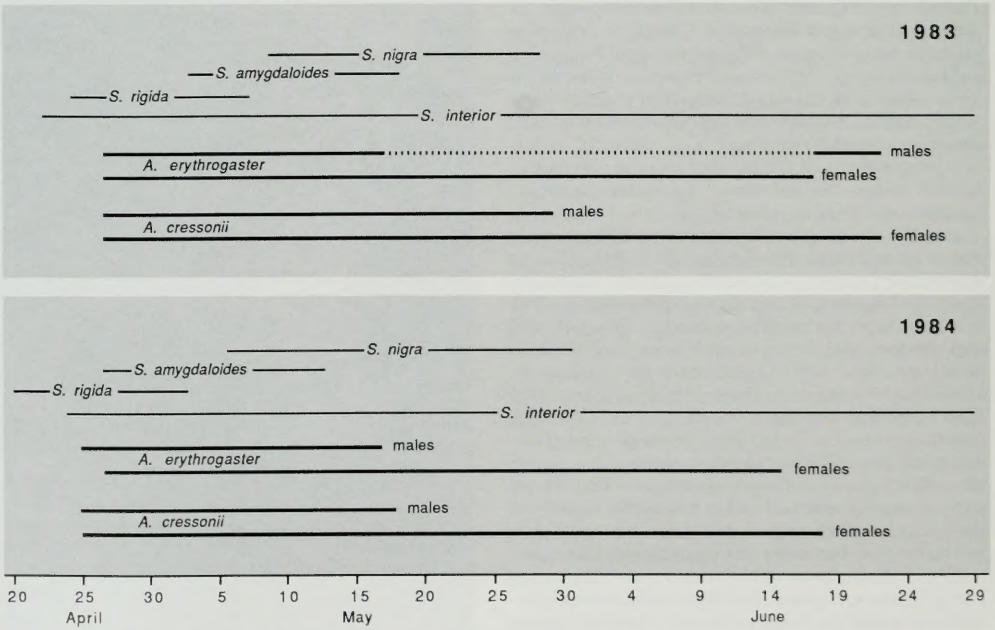


FIGURE 2. Flight periods of *Andrena erythrogaster* and *A. cressonii* during 1983 and 1984 and flowering seasons of the four *Salix* species found near the nesting site. Dashed line for *A. erythrogaster* males (1983) indicates a period that included eight collecting days on which no specimens were taken (see text).

surrounded by moss may have been cushioned against rainfall. Four other nest entrances were well concealed by plants and/or organic debris. Two of these were beneath large, dead leaves and completely hidden from view. All nests at the Homer Lake site were situated within the area of trampled vegetation or just outside it where plants were up to 25 cm tall on 17 May. Most had been dug in small areas of bare soil surrounded by grass tussocks and other plants. Thus, entrances were usually well concealed, especially after their tumuli had been flattened and dispersed by rain and wind. Nests with intact tumuli were more readily visible. One nest was largely concealed beneath a dead leaf. Rau (1935) reported on a perennial aggregation of *Andrena erythrogaster* in his garden in Kirkwood, Missouri. Nests were dug in a footpath and in surrounding grassy areas. In both situations, tumuli were readily visible.

The distance from a nest to its nearest neighbor was variable. Nearest-neighbor distance at Lodge Park varied from 10 to 75 cm. At Homer Lake it ranged from 23 to 190 cm.

The Lodge Park site had been used in previous years as evidenced by the discovery of old cells during 1981 excavations, and bees nested at the site again during 1982. Nine of the ten 1983 Homer Lake nests were excavated, but no cells from previous years were found. During 1984, however, four *Andrena erythrogaster* nests were found at the site.

Each year all nests were found after provisioning had begun, and thus no observations of emergence, prenesting, or excavation behavior were made. Extensive collections from *Salix* spp. during 1983 and 1984, however, showed that few of the females captured early in the season had been collecting pollen. During 1984, no females were taken on the first two collecting days (25, 26 April); on the next three (27, 28 April and 1 May), only 1 of 34 females had a pollen load. On 2 May, however, 27 of 53 females carried pollen, and the proportion of pollen collectors remained high for the rest of the season. A similar trend was noted during 1983. Bees engaged in nest construction and other preprovisioning activities apparently visit nectar sources periodically to maintain their own energy reserves, and the early season, nectar-collecting females seen in 1983 and 1984 may have been at this stage in their life cycles.

Only four nests had largely intact tumuli when found. These tumuli were of similar form, with the entrance placed eccentrically, near the periphery. The entrance tunnel ran through the tumulus at a shallow, downward angle (Figure 3), and there was no turret. Shape and size of the tumuli were somewhat variable, depending in part on the microhabitat in which a given nest had been dug (i.e., in bare soil or surrounded by vegetation). Two tumuli measured 6.0 × 4.5 cm and 4.5 × 3.0 cm along their longest and shortest dimensions, respectively. Rau (1935) described the tumulus of *Andrena erythrogaster* as "conical and roughly about one and one-half to two inches in diameter with an opening at the side or top."

The main burrow in 20 nests (12 from Lodge Park, 8 from Homer Lake) was largely intact at excavation and was traceable, in some cases to the level of the cells. Overall, burrows were of remarkably uniform configuration (Figures 3, 10, 12). Ten burrows entered the soil perpendicular to the surface, or nearly so, and descended almost vertically. The initial 1.0–6.5 cm of the remaining ten were at angles between 50° and 85° above horizontal. Each burrow then made a distinct, if sometimes slight, change in direction toward vertical and continued to descend. The first 6.5 cm of the most unusual of these descended at 55° above horizontal, then bent abruptly and continued downward vertically. Meandering of the main burrow was in most cases restricted to slight deviations from the principal direction of travel, although two nests

FIGURES 3–9. Nest structure and variation in lateral burrows of *Andrena erythrogaster*. Scale refers to all figures. Fig. 3. Nest #1, 1984: vertical section of tumulus, main burrow, and cell 7. Fig. 4. Nest #1, 1984: horizontal plan showing arrangement of cells around main burrow and course of lateral to cell 7. Cell numbers are explained in the text. Fig. 5. Nest #1, 1983: vertical section of lower part of main burrow and lateral burrow to cell. Fig. 6. Same nest as shown in Figure 5, horizontal plan. Fig. 7. Nest #4, 1983: vertical section of lower part of main burrow and lateral burrow to cell. Fig. 8. Same nest as shown in Figure 7, horizontal plan. Fig. 9. Nest #11, 1981: vertical section of lower part of main burrow and lateral burrow to cell.

had two or three more marked bends. As several nests showed, the main burrow bent toward the horizontal upon reaching the depth of the cells, continued for a variable distance, and ended in a cell (see discussion of lateral burrows below).

The main burrow was circular in cross section and of uniform diameter in a given nest. Ten of 20 nests had burrow diameters of 7–8 mm. The others were slightly smaller or larger. The two narrowest burrows were 6–7 mm in diameter and the widest was 8–10 mm. Irregular, shallow grooves, probably cut by the bee's mandibles during excavation, roughened in places the main burrow of most nests.

Cells were constructed singly at the ends of lateral branches off the main burrow. After provisioning and oviposition were completed, a cell was closed and the lateral burrow leading to it was plugged with soil so that its course could rarely be traced accurately. In ten instances, however, either the lateral to the most recently constructed cell had not yet been plugged or the lateral to a closed cell was traceable because the plug of soil was loose or of a color different from that of the surrounding soil. Generally, the transition from main to lateral burrow was abrupt as the nearly vertical main burrow bent toward the horizontal. The path taken by the lateral to the cell was variable (Figures 3–9). In some instances, the lateral was nearly horizontal (Figure 9); in others, it descended at a marked angle, the steepest about 55° above horizontal (Figure 3). Angle of descent was not always uniform throughout the length of a lateral. Viewed from above, some laterals followed a nearly straight course to the cell (Figure 8) and others had one or more distinct bends (Figures 4, 6).

Laterals generally had smaller diameters than the main burrow. For example, the diameter of the lateral leading to cell 7 in nest #1 (Homer Lake, 1984) decreased from 7–8 mm near the main burrow to 5.5 mm just before the cell. Other laterals narrowed similarly along their lengths. The lengths of the ten laterals that were traced varied from 3 cm to just over 7 cm. The horizontal distance from a given cell to the actual or approximate position of the main burrow at the depth of that cell was measured for 74 cells. Although this distance did not always represent the actual length of the lateral burrow, it was a close approximation because the main burrow in most nests descended almost vertically. Mean distance from the main burrow for the 74 cells was 6.3 cm (range: 3.0–9.5 cm). The lengths of the ten laterals that were measured fell within this range.

Cells from nests at Lodge Park ranged from 12.5–25.0 cm below the soil surface, with a mean depth of 17.4 cm (N = 29). Mean cell depth at Homer Lake was 23.8 cm (N = 74; range: 14.5–31.0 cm). This difference may have been due in part to soil conditions at the two sites. The woodland soil at Lodge Park was heavy, well compacted, fine grained, and rather clayey with numerous small (2–4 mm in diameter) pebbles throughout. The nesting site at Homer Lake was on the floodplain of the Salt Fork River. An abundance of roots and rootlets ran throughout the upper 7–8 cm of the soil, and some reached cell depth. The upper 7–9 cm of soil was dark grey to black and fine grained and probably represented accumulated layers of silt deposited during periodic flooding of the river. Below 9 cm, the soil changed to light brown or tan and was much more sandy. The sandy layer extended to the depth of the cells and below. Overall, the soil at Homer Lake seemed lighter and more friable than the soil at Lodge Park. Perhaps bees found excavation at Homer Lake easier and so tended to dig deeper nests. Malyshev (1935) noted that *Colletes cunicularius* L. dug its nests deeper in loose sand than in hard soil.

The range in cell depth within a given nest was generally small. The deepest cell in eight of ten nests from Homer Lake (1983 and 1984) was at most only 5 cm deeper than the shallowest. Each of the eight nests contained 6 to 13 cells. One of the other two nests, #5 (1983), contained 7 cells, the shallowest at 14.5 cm and the others between 24.0 and 26.5 cm deep. Nest #9 (1983) had 11 cells, 2 between 15.5 and 20.0 cm deep and the others 23.5 to 27.0 cm deep. The range in cell depths within nests at Lodge Park was also narrow. The single nest excavated in 1982 contained 9 cells between 16 and 21 cm deep; the maximum difference in depth between cells in a given 1981 nest was 6.5 cm.

The main burrow was not found to extend below the deepest cell. In those nests where it was open for its entire length, it gave rise to a lateral burrow at its lower end. Apparently the main burrow is excavated to a certain depth, at which point the first lateral is extended from it. Subsequent laterals branch off the main burrow a few centimeters above or below the first, a pattern of ramification Malyshev (1935) termed stationary.

Fourteen nests were excavated at Lodge Park during 1981, the first on 2 June. By that date only one of the ten bees that had been under observation since the end of April was still active and provisioning. Eleven nests contained 1–5 cells, and no cells were found in the other three. Although some cells may have been missed during excavation, fewer cells were probably provisioned per nest during 1981 than in subsequent years.

Weather during late April and May 1981 was frequently cool and rainy. United States Weather Bureau records from the Urbana weather station (32 km east of Lodge Park) showed that 15.3 cm of rain fell during April (5 cm above normal), although the average temperature (13.5°C) was 2.2°C above normal. Rainfall at the Monticello station (3.2 km south of Lodge Park) totaled 13.05 cm (temperature not recorded at Monticello). During May, 14.8 cm of rain (4.3 cm above normal) fell in Urbana (16.2 cm at Monticello); the

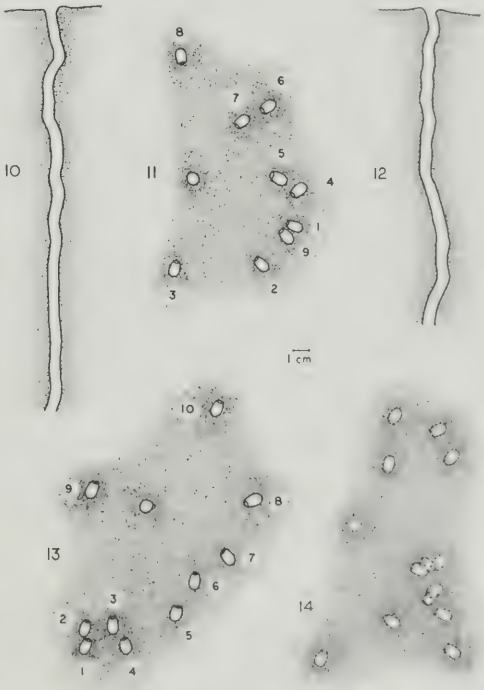
average temperature, 14.8°C, was 2.2°C below normal. All but 0.6 cm of rain in Urbana and 0.7 cm in Monticello fell during the first 20 days of the month. Thus, during late April and the first two-thirds of May, a period encompassing the bulk of *Andrena erythrogaster*'s active season, many days were unsuitable or suboptimal for foraging. Conditions improved during the last 10 days of May, but by the 24th only three of the original ten bees were still active. Weather conditions certainly limited foraging activity during April and May, and the number of cells provisioned must have been reduced as a result.

In contrast, only 6.2 cm of rain (4.1 cm below normal) fell in Urbana during April 1982 (5.1 cm in Monticello), although temperatures were also below normal. During the first 16 days of May, only 2.2 cm of rain were recorded in Urbana and 1.8 cm in Monticello; temperatures were well above normal. Highs in Urbana ranged between 22.0°C and 31.5°C, with a single exception of 19.5°C on 7 May. These conditions resulted in optimal foraging weather for bees. The nest excavated on 17 May contained one unprovisioned and eight provisioned cells. Three and probably a fourth contained provisions and eggs, indicating that they had been recently provisioned. This bee had made good use of favorable weather.

Nine nests were excavated at Homer Lake during 1983 after resident female bees had become inactive. I am confident that few, if any, cells were missed during these excavations. The mean number of cells per nest was 8.3 (range: 6–13). A single nest was excavated during 1984 (21 May) while the bee was still active. Her nest contained 1 unprovisioned and 6 provisioned cells, all of which contained eggs and provision masses.

Viewed from above, the cells in a given nest were variously distributed about the main burrow (Figures 4, 11, 13, 14). Often, a rather large, contiguous sector with the main burrow as its center contained no cells (Figure 11, for example). The cells shown in Figures 4, 11, and 13 are numbered consecutively in the presumed order of construction; exceptions are noted in the discussion that follows.

Based on the stage of development of immatures found in the cells at the time of excavation, the sequence of cell construction in three Homer Lake nests was roughly determined. In nest #2 from 1983 (Figure 11), cell 8 was at the end of an open lateral, partly provisioned, and therefore the newest cell. Cell 7 contained a small larva (possibly a first instar), cells 6 and 5 also held small larvae, and cell 4 contained a partly grown larva. Cell 1 and cell 2 each contained a large, fully fed larva, and cell 3 held one that was half-grown. Cell 9 was not found until much later but may have been built about the time of cells 1 and 2. Cells 1 and 2 appeared to have been provisioned first followed by cell 3. The bee then worked generally counterclockwise in building cells 4 to 8. Nest #8 (Figure 13) was excavated on 12 June 1983. The adult bee was found dead in the nest but had been alive on 9 June. Cell 9 contained an egg and was perhaps the newest although 8 also held an egg. Cell 7 contained a small larva; 6 and 5, medium-sized larvae; 4, a large larva and some pollen; and 1, a fully fed larva. Cells 2 and 3 were not found until much later, but if they were provisioned about the same time as cells 1 and 4, cell construction would have proceeded in a generally counterclockwise direction about the main burrow. The chronology of cell 10 was problematical because it contained a moldy provision mass. Finally, nest #1 from 1984 (Figure 4) was excavated on 21 May when the adult was still active. Cell 7 was unprovisioned and therefore the newest. All others contained eggs, but the egg in cell 1 hatched first (22 May), probably making that cell the oldest. This bee may have worked

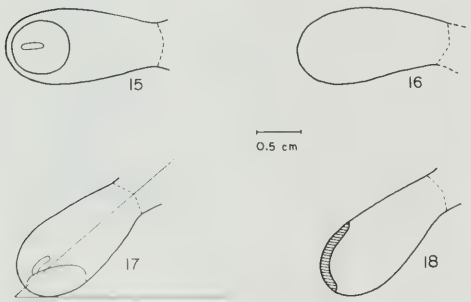


FIGURES 10–14. Nest structure of *Andrena erythrogaster*. Scale refers to all figures. Fig. 10. Nest #2, 1983: vertical section of main burrow. Fig. 11. Nest #2, 1983: horizontal plan showing arrangement of cells around main burrow. Cell numbers are explained in the text. Fig. 12. Nest #8, 1983: vertical section of main burrow. Fig. 13. Nest #8, 1983: horizontal plan showing arrangement of cells around main burrow. Cell numbers are explained in the text. Fig. 14. Nest #9, 1983: horizontal plan showing arrangement of cells around main burrow.

clockwise during cell construction, beginning with cell 1 and ending with cell 7.

If the order of construction hypothesized for cells in these three examples is correct, bees may tend to maintain a generally clockwise (Figure 4) or counterclockwise direction (Figures 11, 13) around the main burrow as they build cells. One advantage of such behavior is that new cells would be less likely to break into previously constructed cells. On the other hand, cells were at times built very close together, either side by side or one above another, and separated by a centimeter or less of earth (Figure 14, for example). Other cues, therefore, may be involved in maintaining minimum intercell distance.

The cells of *Andrena erythrogaster* were elongate and bilaterally symmetrical, although not always perfectly so (Figures 15–18). They were narrowest at the cell closure, expanded gradually to their maximum diameter about two-thirds along their lengths, and were broadly rounded at their distal ends. The mean length of 20 cells from Homer Lake was 14.4 mm (range: 13.3–15.4 mm) as measured along the longitudinal axis from the distal end of the cell to the point where cell closure met cell wall. The mean length of 8 cells from Lodge Park was nearly the same, 14.5 mm (range: 12.7–15.4 mm). Maximum diameter of 20 cells from Homer Lake ranged from 6.8–7.7 mm (mean = 7.2 mm); 11 cells from Lodge Park ranged from 6.7–7.5 mm (mean = 7.1 mm). Minimum cell diameter (near the closure) ranged from 3.9–4.7 mm (N = 16; mean = 4.4 mm) for cells from Homer Lake and 4.2–4.8 mm (N = 7; mean = 4.5 mm) for cells from Lodge Park. The shape of the cell in sagittal section (Figures 17, 18) was slightly different from its shape in frontal section (Figures 15, 16). Whereas the right and left walls of the cell were generally of similar curvature, the roof of the cell was often somewhat flattened compared to the more rounded cell floor. The walls of the cell were smooth and slightly shiny but did not appear to have been plastered with soil from elsewhere in the nest. They were coated with a thin, waterproof lining that extended to the cell closure but little, if any, beyond it. A spiral arrangement of soil particles with 3–5 rows to the radius formed the cell closure. It was markedly concave on the cell-facing side and absorbed water readily. The longitudinal axis of the cell was always at a substantial angle, the mouth of the cell uppermost. This angle, measured with a protractor above a horizontal line tangent to the lowermost point of the cell, varied from 27° to 53° for 13 cells and fell between 35° and 45° for 9 of those cells.



FIGURES 15–18. Cells of *Andrena erythrogaster*. Scale refers to all figures. Fig. 15. Frontal section through a nearly symmetrical cell with position of pollen mass and egg shown. Fig. 16. Frontal section through a rather asymmetrical cell. Fig. 17. Sagittal section through a cell with position of pollen mass and egg shown. Angle of the cell (41°) is typical for cells of this bee. Fig. 18. Sagittal section through a cell showing position of the fecal deposit (hatched lines).

Behavior of Females at the Nest

Observations of bee behavior at the main nest site in Lodge Park were made on 17 days between 26 April and 1 June 1981. Three days of observations were made during 1982 at the same site, and 7 days were spent at the Homer Lake site during 1983.

The time at which *Andrena erythrogaster* females began foraging varied from day to day and was much influenced by weather. On warm, sunny mornings some bees began foraging well before 0900. Cool and/or cloudy weather delayed the onset of foraging until later in the morning or into the afternoon. Variations were also observed from bee to bee on a given day. Foraging activity tapered off in the afternoon, again depending on the weather, but on warm, sunny days some bees continued until after 1800. On 21 May 1983, for example, one of the observed bees returned with a pollen load at 1850 and another was still out on a foraging trip.

Prior to leaving on foraging trips, bees spent variable lengths of time sitting in their nest entrances. Especially long periods were spent there before the first departure of the day and on days with poor weather. Usually a bee sat just below ground level, facing outward with her antennae directed forward at a slight, diverging angle. Over the next several minutes or up to an hour or more, the bee gradually emerged from the nest a step or two at a time. Often she moved her head from side to side prior to a short advance. Not infrequently a bee retreated down her burrow for a few seconds to a minute or more. Such retreats were of two forms. Most commonly, the bee dropped quickly out of sight after a disturbance such as an abrupt movement by the observer, a shadow falling across the burrow, or a passing insect. Very small (2–3 mm) beetles and ants passing the entrance were at times sufficient to induce a hasty retreat. At other times, the bee backed slowly and methodically down the burrow for no apparent reason. Eventually, however, the bee emerged completely.

Rather than take immediate flight, an emerging bee usually crawled a few centimeters from the entrance, often turned partway around (sometimes facing the nest), and then took wing. On cool days, bees tended to crawl greater distances and often basked in patches of sunlight on the forest floor. Dead leaves illuminated by the sun seemed to be favored basking places. On three occasions, bees were observed to fly to sunlit leaves 2–3 m above the ground and sit in the sun. Bees generally spent less time in the nest entrance prior to subsequent foraging trips and during fair weather. Similar behavior has been observed for other *Andrena* (Schrader and LaBerge 1978; Davis and LaBerge 1975).

Bees made orientation flights when leaving the nest after it or its surroundings had been disturbed (usually by the observer) and at other times, most frequently on the first trip of the day. During observations at Homer Lake in 1983, 114 nest departures were seen; 22 of them included orientation flights. Such flights varied in length from 4 or 5 seconds to lengthy affairs lasting 20 seconds or more. From a position a few centimeters away from the nest, a bee faced her nest and took flight. Hovering a few centimeters above ground, she began to swing back and forth in short arcs with the nest at their center. Gradually she increased height, distance from the nest, and length of the arcs. Flight speed also increased and finally she was lost from view. Orientation flights appeared similar in form to those described for *Andrena* (*Leucandrena*) *erythronii* Robertson (Michener and Rettenmeyer 1956).

Bees generally appeared to have little difficulty locating their nests upon returning from foraging trips. A bee would be seen flying rapidly in the vicinity of the nest site. After one or two passes through the area, she would localize near her nest and land a few centimeters from it. She then crawled promptly to the nest and entered. Occasionally a bee landed farther from the nest and, after crawling around briefly, took flight again. Her second landing was usually closer to the nest, whereupon she crawled inside. This behavior gave the impression that a close aerial approach was required for swift location of the nest from the ground. When returning bees had difficulty locating their nests, they engaged in more extensive flights over their nest sites (these resembled orientation flights). After landing, they crawled about before either finding the entrance or taking flight again. A number of instances were noted in which a bee departed from or returned to her nest along nearly the same route two or more times in succession.

During some of my first observations of *Andrena erythrogaster*, I noted an interesting behavior after a bee had returned from a foraging trip and entered her nest. Within several seconds, not long enough to have deposited her pollen load, she reappeared in the entrance at ground level or just below, facing outward. After sitting in the entrance for some time, she retreated, not to be seen again until she left on the next trip. This behavior was observed at least once in six of the ten bees under observation at Lodge Park in 1981. During 1983, the presence or absence of this behavior was noted after each return, including how much time elapsed between entry and reappearance and approximately how much time was spent in the entrance. Two of nine bees were never observed in this behavior, but their nests had partially intact tumuli and had those bees assumed the usual position, they could not have been seen. One of the other seven bees exhibited this behavior after fewer than 50 percent of her returns to the nest. The other six sat in their nest entrances on 63 of 71 occasions (89%) after returning from foraging trips. In 55 instances, the time elapsed between a bee's entering her nest and her return to the entrance was obtained and ranged from 3 to 100 sec; on 39 of these occasions, the time was between 7 and 17 sec.

The approximate time a bee spent in her nest entrance before retreating was recorded in 56 cases. Times were not exact because I could not watch a single bee continuously and still observe the other nests. The bee, therefore, was checked periodically (every 15–20 sec) until she backed down into her burrow. Time spent in the nest entrance ranged from about 50 seconds to more than an hour. Usually, however, the time was less than 10 minutes, distributed as follows: less than 1 min (5 occasions); 1–2 min (12); 2–3 min (6); 3–4 min (3); 4–5 min (4); 5–6 min (5); 6–7 min (5); 7–8 min (4); 9–10 min (2). On the remaining ten occasions, more than 10 minutes were spent in the entrance. Nine of these ten occasions occurred near the end of the day when the bee under observation may have completed foraging.

Considerable data were obtained concerning the durations of the foraging trips of *Andrena erythrogaster*. During 1981, screen cone traps were not used to cover nest entrances, and bees were allowed to leave and enter freely. This system made it difficult to follow the activities of up to ten bees simultaneously, and errors may have occurred if departures and enterings were missed. Seventy-nine pollen-collecting trips were timed to the nearest 0.5 min for a mean trip duration of 103.0 min (range: 46.5–202.0 min). The nest of a single bee was watched for three consecutive days during 1982. Sixteen pollen-foraging trips were accurately timed and ranged from 20.5 to 85.0 min (mean = 48.0 min). I strongly suspect that this bee had been exploiting *Salix nigra* as a pollen source because of the color of her pollen loads and because this willow was in bloom at the time. Finally, the lengths of 82 trips for *S. nigra* pollen and 11 for *S. interior* were timed to the nearest second during 1983. Reliable data were obtained for as many as nine nests at a time because cone traps were placed over the nests at all times except to allow bees to enter and leave. Identifi-

cation of pollen sources was by color. No other willows were in bloom at the time, and both species were present within 50 m of the nest site. Mean trip length for *S. nigra* pollen was 58 min 54 sec (range: 13 min 45 sec–176 min 50 sec; S.D. = 28.82); that for *S. interior* was 78 min 1 sec (range: 53 min 20 sec–113 min 41 sec; S.D. = 21.90). Foraging trips to *S. nigra* were significantly shorter ($0.01 > p > 0.001$; Wilcoxon two-sample rank test), and bees preferred it as a pollen source when both it and *S. interior* were in flower simultaneously (Miliczky 1985).

Bees, on occasion, returned without pollen loads and presumably had collected only nectar. Twenty-one such trips timed during 1981 had a mean length of 139.5 min (range: 63.5–257.5 min). The mean length of seven nectar-collecting trips during 1983 was 102 min 31 sec (range: 26 min 38 sec–144 min 45 sec). Both years the mean length of a nectar-collecting trip was substantially longer than that of a pollen-collecting trip.

Time spent within the nest between foraging trips averaged 23 min during 1981 (N = 60; range: 13–57 min). The single bee observed during 1982 spent, on average, 18 min within the nest between trips (N = 13; range: 12.5–35.5 min). The average stay in the nest during 1983 was 29 min 48 sec (N = 79; range: 9 min 21 sec–111 min 48 sec). Usually the bulk of the time between trips was spent inside the nest, out of sight. Presumably, a principal activity during this time was the removal of pollen from the scopae. The minimum time required to remove a pollen load may be on the order of 9 minutes, based on the shortest recorded stay in the nest between trips (9 min 21 sec) and assuming that unloading the scopae required most of that time.

Bees did not always thoroughly clean their scopae of pollen after each trip, and they often appeared dusted with the substance (sometimes quite heavily) when they left the nest. Prior to departure on foraging trips on 23 May 1983, seven bees were carefully checked at least once for pollen dusted on the body. The three bees that were checked before their first trip of the day were found to be clean and free of pollen; however, five bees were checked for residual pollen on eight occasions after having completed at least one pollen-collecting trip, and all were found to have noticeable dustings on their ventral surfaces, scopae, and faces. If one assumes that this pollen was still viable, such a bee was a potential pollinator even if she did not first visit male willows on her next trip.

The number of pollen loads needed to provision a cell was not determined. Linsley and MacSwain (1959) estimated a minimum of four loads for the provision mass of *Andrena caerulea*, and *A. erythrogaster* probably requires at least as many, in addition to a substantial amount of nectar. Even during favorable weather, an individual bee was observed to collect a maximum of seven pollen loads in a day and this observation was made only once, on 14 May 1982. The weather was sunny with temperatures ranging from 23°C–29°C, and the bee collected the seven loads of pollen (probably *Salix nigra*) between 0915 and 1704. Six loads of *S. nigra* pollen collected by a bee on 21 May 1983 took over 8 hours to gather. Five or fewer pollen loads per day was the usual number, an observation that suggests that more than one cell is unlikely to be provisioned in a given day. The nest entrance was not plugged with soil during foraging activities.

No evidence was found that individual bees constructed more than one nest per season. At the time of excavation, seven bees were found dead in their nests.

Provision Mass and Immature Stages

The provision mass was placed at the lower end of the cell and was in the form of a flattened sphere (Figures 15, 17, 19, 20). Viewed from above, the mass was nearly circular. Measurements were taken of five masses. Lengths ranged from 5.0–6.5 mm. Widths ranged from 5.5–6.0 mm and, with a single exception, were about 0.5 mm less than lengths. The exception was 5.0 mm long by 5.5 mm wide. Because pollen masses could not be lifted intact from their cells, thickness (i.e., at right angles to the cell's long axis) was estimated as 2.5–3.0 mm. The upper surface was gently rounded and in one case appeared to have a very slight depression in the center. Nectar content of the provision mass was high, giving it a mushy, porridgelike consistency. While the mass held its shape as it rested in the cell, it yielded under slight pressure from a forceps and could not be picked up. Clear, sticky liquid (nectar) was present between the cell walls and the periphery of the provision mass; the amount varied somewhat from cell to cell. The provisions had a faint odor detectable from within 5–6 cm.

The posterior end of the egg was inserted into the upper rear surface of the provision mass. Point of insertion was about 1 mm from the rear edge of the mass. One egg had been inserted 0.16 mm into the surface of the provisions, and a definite depression was left when it was removed. The egg was white, somewhat translucent, and gently curved; it was positioned so that its anterior end was directed toward the mouth of the cell. Eggs measured 2.3–2.4 mm in length (tip to tip) and had a maximum thickness of 0.65 mm. Thickness varied but little along the length of the egg. The posterior end was somewhat blunter than the anterior.

Duration of the egg stage was not determined precisely but probably extends for several days. This conclusion is based on extrapolated information from the 1984 Homer Lake nest (see above) that had six cells with eggs and provision masses at the time of excavation. If this bee had provisioned one cell per day dur-

ing the fair weather prior to excavation, the oldest egg would have been at least 7 days old when the nest was dug. One egg hatched the day after excavation. If this egg was the first egg laid, it was at least 8 days old. One egg hatched on each of the next 2 days. Time from oviposition to hatch, therefore, may be on the order of 8–10 days. Stephen (1966) reported a similar length of time (8–12 days) before egg hatching in *Andrena* (*Tylandrena*) *perplexa* Smith.

The segmented nature of the larva became visible through the chorion just prior to hatching, and the egg tended to drop down onto the provisions along its full length. In two cases, a number of small beads of moisture appeared on the surface of the egg prior to eclosion. The amount of free liquid around the provision mass increased substantially between the discovery of a cell and the early larval stages. In some cases, liquid eventually covered much of the provision mass. Provisions having a very moist, almost soupy consistency may be necessary for the survival of young larvae. In five instances where free liquid flowed out of damaged cells and caused noticeable drying of the provisions, the young larvae failed to survive and may not even have begun to feed.

Development from egg to fully fed larva is shown in Figures 19–25 for a larva from the 1984 Homer Lake nest. Observations of this larva provided much of the information for the following description of feeding behavior. The newly eclosed larva lay atop the provision mass—its head near the center, its tail near the posterior edge—and began to feed in the region beneath its head. It remained in a similar position during much of its development. When actively feeding, it sometimes entirely submerged its head into the provisions. At other times, its head was raised completely above the surface for variable lengths of time. As its length increased, its head moved forward on the provisions so that the larva fed progressively nearer the front of the mass; the posterior end made contact with the rear wall of the cell. The larva also sank slightly into the surface of the provisions. A shallow feeding depression was at times visible in the provisions beneath the larva's head. As feeding continued and size increased, the larva remained atop the provision mass and eventually obscured much of the remaining food beneath its body (Figure 23). By this time, the free liquid had largely been consumed. A day or two before completion of feeding, the larva came to lie more or less on its side, curled around the remains of the provisions, which adhered to the floor of the cell and to the larva's ventral surface. The larva was quite mobile at this stage and could change its position in the cell. Several larvae came to lie with their heads near the rear of their cells and their tails near the mouth of their cells by the time they had completed feeding. This position was not taken by the larva shown in Figure 25. Eclosion took place between 23 and 24 May, and this larva completed feeding by 2 June, about 9½ days later. More than half of its provisions were consumed during the last 3 days of feeding, and size increase was rapid during that period.

All observations on larval behavior were made in the laboratory at room temperature (21°C–26°C), but developmental rates are likely to be slower at the cooler temperatures found underground.

Prior to defecation, those larvae that were positioned with their heads near the rear of their cells reoriented themselves so that their heads were near the mouths of their cells. The first fecal material was deposited by three larvae 12 or 13 days after they had finished feeding. Incomplete data for four others indicated that at least 9 days elapsed between the two events. Forty-three larvae excavated between 27 June and 11 July 1983 included 29 postdefecating forms, 13 fully fed, predefecating forms, and 1 small larva on a provision mass.

Feces were deposited on the upper rear wall of the cell (Figure 18) as slender strands 2–5 mm long and about 0.5 mm in diameter. Defecation required 2–3 days, and 30–40 fecal strands were deposited in two or three layers. The postdefecating larva lay on its dorsal surface with its head near the mouth of the cell and its tail near the rear of the cell.

Time from completion of defecation to pupation for 7 larvae from 1983 nests ranged from 56 to 69 days. Minimum time spent as a postdefecating larva for 16 others ranged from 53 to 77 days. These 23 larvae pupated between 25 August and 11 September 1983. Ten larvae from 1981 nests pupated slightly earlier—between 11 and 25 August of that year. All data are from laboratory rearings.

The new pupa was entirely pale, but within 24 hours the ocelli began to take on a faint purplish hue. Soon after pupation the abdomen could be moved in a ball-and-socket fashion about the petiole. Two to three days after pupation, the compound eyes began to darken, the tips of the mandibles began to turn light brown, and a faint but distinct dark region became visible internally beneath abdominal sternites 2, 3, and 4. General darkening of the body began 10–12 days after pupation, and the hair sockets of the legs and abdomen were among the first structures to become distinctly visible. The head and thorax took on a grayish tone and the abdomen turned faintly yellow or amber. Darkening of the legs and antennae proceeded from base to apex, but the reverse was true for the mandibles. As final adult coloration approached, the appendages became capable of movement.

Four or five days prior to emergence, the pupal cuticle began to collapse around the adult as the fluid between the two began to disappear. About a day before emergence, most of the fluid was gone and the pupal cuticle clung loosely around the pharate adult. Adults emerged 19–27 days after pupation in 1983

(N = 16; mean = 22.5 days), between 13 September and 2 October. Data for 1981 were similar; the period between pupation and adult emergence lasted 22–25 days (N = 6; mean = 23 days) with emergence occurring between 3 and 18 September. The wings expanded rapidly but required 2–3 days to harden completely.

Adults overwinter underground in their natal cells, as is the case for other *Andrena* (Michener and Rettenmeyer 1956; Stephen 1966; Davis and LaBerge 1975).

Predators, Parasites, and Associates

Two species of parasitic bees in the genus *Nomada* (Anthophoridae) visited the nests of *Andrena erythrogaster* at Lodge Park during 1981. *Nomada obliterata* Cresson was first seen on 26 April, on which day a female parasite was marked with paint to facilitate observation. The next day two conspecifics were captured and marked. These three individuals were the only *N. obliterata* seen to visit the nesting site during the season. They were very active on 26, 27, and 28 April and visited many of the nests under observation; thereafter, they made few appearances. One of these marked bees was recaptured on 3 May and retained for identification; neither of the others was seen after this date. On 20 May a second and larger species of *Nomada* visited one of the *Andrena erythrogaster* nests. Subsequently she was captured, marked, and released. This bee visited the nest site on 22, 24, 25, 27, and 28 May. Unfortunately, she was not recaptured for identification. A *Nomada* larva was found in 1 of the 20 cells taken from the 1981 nests. Although *Nomada* were seen in the vicinity of the nest site during 1982, none visited the nest under observation. No parasitic bees were seen at the Homer Lake nesting site. The behavior of the *Nomada* parasites will be reported in a separate publication.

Meloe (Coleoptera: Meloidae) larvae prey on the larvae of wild bees (Mayer and Johansen 1978), and a *Meloe* larva (det. J.K. Bouseman) was found during the excavation of one of the 1981 nests. The larva was in a rough, oval-shaped cavity about 1 cm in length, 12 cm below the surface. About 4 cm from the *Meloe* larva was an *Andrena erythrogaster* cell (depth = 14 cm). The cell contained the remains of a provision mass and some debris and appeared to have been broken open, perhaps by the departing *Meloe* larva. A similar discovery was made in one of the 1983 nests. A *Meloe* larva was found in a cavity about 24 cm deep. Two of the six cells in the nest contained soil and pollen mixed together and had apparently been plundered by the *Meloe*. One of the cells was about 3 cm from the *Meloe*, the other about 4 cm. Mayer and Johansen (1978) found that during development *M. niger* Kirby consumed two or more *Nomia melanderi* Cockerell larvae (Hymenoptera: Halictidae). The 1983 larva had apparently completed feeding because it later yielded an adult male *M. americanus* Leach (det. J.K. Bouseman).

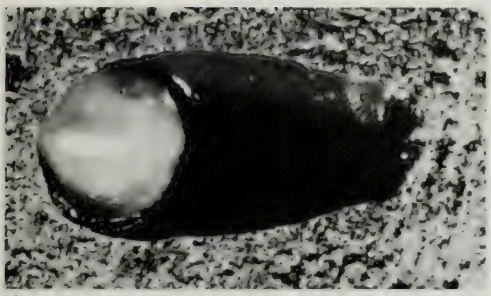
On a number of occasions in 1983 and 1984, unidentified mutillids (possibly *Dasymutilla* sp.) were seen in or near nest entrances; however, no evidence of successful depredation by velvet ants was found.

A specimen of the robber fly, *Laphria thoracica* Fab. (Diptera: Asilidae; det. D.W. Webb), was taken with a female *Andrena erythrogaster* as prey on 13 June 1983 at Homer Lake. This fly, considerably larger than *A. erythrogaster*, is a bumblebee mimic and was spotted resting on vegetation at the edge of the main stand of willows, about 35 m from the nesting site.

Several other organisms were seen to interact with female bees at nest sites, the most unusual of which were slugs. At 0935 on 27 April 1981, a bee returned to her nest with a pollen load. She was seen in the nest entrance 20 minutes later, abdomen outward, and had not deposited her pollen. At 1248, nearly three hours later, her abdomen was again observed in the entrance, and she was behaving strangely. During the next 18 minutes, she repeatedly entered the burrow only to back out shortly, grooming on a number of occasions. Finally, at 1306 while the bee was out of her nest, a slug 2 cm long emerged from the burrow. The bee returned to her nest and seemed none the worse for her experience. On two other occasions, slugs were observed leaving or about to enter nests.

On 28 April 1981, a marked *Nomada obliterata* emerged from one of the *Andrena erythrogaster* nests and sat in the entrance. A spider (probably a wolf spider) sitting nearby began moving toward the bee. The spider lunged and a brief struggle ensued, but the bee broke away and flew off. On another occasion, an *Andrena erythrogaster* was sitting just within her nest entrance prior to departure when a spider ran over her burrow and stopped momentarily before moving on. Later the same day a tiger beetle (*Cicindela* sp.) ran to the nest entrance and poked the piece of vegetation that I had used to loosely plug the burrow. The bee was in her nest and left shortly thereafter. Tiger beetles were not uncommon around nest sites and along with large, ground-dwelling spiders are at least potential predators of bees in or near their nest entrances.

Various species of ants entered or were active around bee burrows on a number of occasions. Once or twice they caused bees sitting in their nests to retreat, but no evidence was found that ants plundered bee cells. On one occasion a centipede 2 cm long emerged from a nest shortly after the bee returned with a pollen load. The bee was not harmed.



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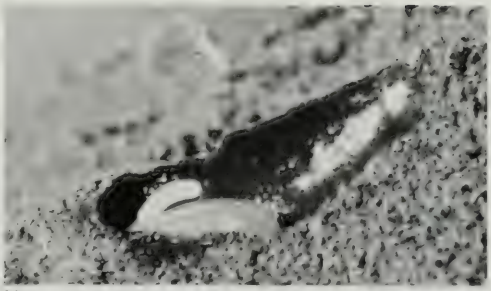

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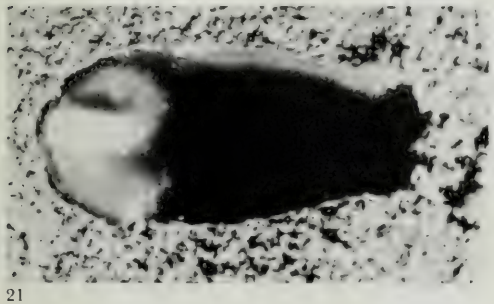

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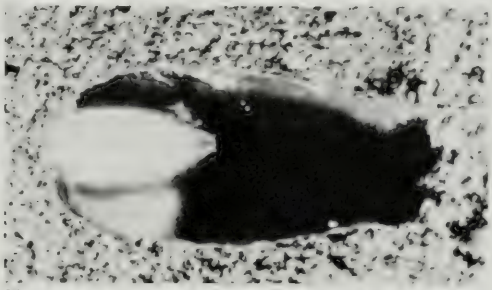

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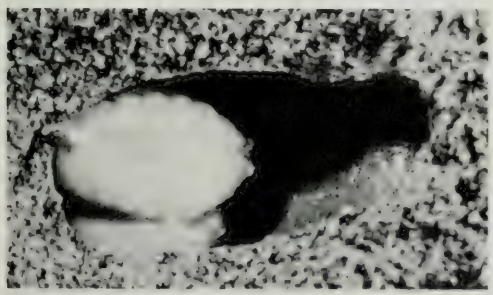

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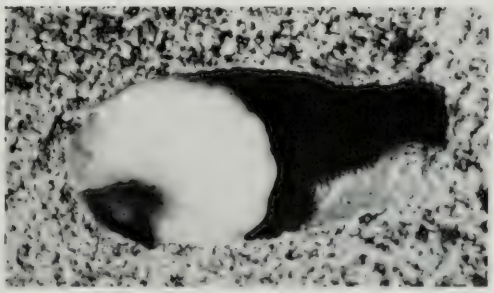

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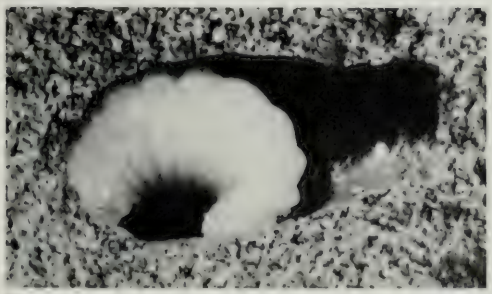

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FIGURES 19–25. Egg placement and larval development of *Andrena erythrogaster*. Fig. 19. Cell with provision mass and egg seen from above. Fig. 20. Cell with provision mass and egg seen from the side. Fig. 21. Small larva atop provision mass. Fig. 22. Medium-sized larva atop provision mass. Fig. 23. Large larva atop provision mass. Note that increase in size was accompanied by relatively little change in position. Fig. 24. Nearly fully fed larva lying on its left side, curled around the remains of the provisions. Fig. 25. Fully fed larva (predefecating) lying on its left side, its head toward the mouth of the cell.

Observations on Other *Andrena* Species

The following observations on *Andrena personata* and *A. cressonii* include the first descriptions of nest structure for either species and also the first for a North American member of their respective subgenera. *Andrena personata* and other *Micrandrena* are small bees, but various species can be very abundant locally. *Andrena* (*M.*) *nigrae* and *A.* (*M.*) *ziziae* Robertson, for example, were especially common at Homer Lake as was the widespread *A. cressonii.*

Andrena (*Micrandrena*) *personata* Robertson

This small bee (5.5–6.0 mm in length) was common at the wooded nest site in Lodge Park, and several nests were found during 1981 and 1982. Its presence was first noted on 30 April 1981, when males were seen in flight at the nesting site. Males flew about flowers and vegetation and low over the ground, occasionally pouncing on one another and on other insects. They often seemed to aggregate in sunny areas. Similar activity was observed on 30 April and on 2, 3, and 4 May.

The first nests were discovered on 25 May 1981 by noting the return of pollen-laden females. Nests were in the same area as those of *Andrena erythrogaster*, and some were located within a few centimeters of those of the larger bee. Entrances were well concealed because of their small size (2.5–3.0 mm in diameter), their placement near or beneath vegetation and/or organic debris, and the fact that most lacked a tumulus at the time of discovery. One nest beneath a dead leaf had a largely intact tumulus in the form of a hill of soil 1.5–2.0 cm in diameter. During 1982, nesting females were found on 14 May.

Andrena personata seems to be a polylectic species with preferences for rosaceous, umbelliferous, and salicaceous plants (Ribble 1968). Pollen sources of the Lodge Park population were not determined, but both yellow and white pollen loads were noted. Eleven pollen-collecting trips were timed and lasted from 31.5–118.5 min (mean = 83.0 min). One trip, apparently for nectar, lasted 129.0 min. Length of stay in the nest between trips averaged 11.5 min (N = 6; range: 8.5–14.0 min).

A nearly complete excavation, except for three short sections of the main burrow, was made of one nest (Figure 26). The initial 2.5 cm of the burrow were not intact, but the burrow then descended almost vertically, with a few shallow bends (once to avoid a small stone), to nearly the level of the cells. The burrow was lost for a short distance at a depth of 21.5 cm, and the first cell was found 22.5 cm below the surface. Subsequent cells were at depths of 23.5, 24.0, and 25.5 cm. The main burrow ended in a slightly enlarged cavity at a depth of 28 cm. Two other cells, probably associated with this nest, were at depths of 27 and 28 cm but are not shown in the diagram. All but one cell contained postdefecating larvae at excavation, and that one lacked a larva but contained some pollen and was infested with mites. Feces were deposited on the upper rear walls of cells as in *Andrena erythrogaster.* The small, ovoid cells had their long axes oriented at a shallow angle, the mouth of the cell higher than the rear. The main burrow was circular in cross section and 2.5–3.0 mm in diameter throughout its length. Partial excavation of a second nest revealed four cells at depths between 16.5 and 19.6 cm.

A very small, unidentified species of *Nomada* was observed several times at the nesting site and is likely a parasite of *Andrena personata.* Parasites flew slowly over the ground, often less than 2 cm above the surface, landing occasionally to investigate holes, cracks, and small piles of debris. Once, a *Nomada* entered a nest, backed out five to six seconds later, crawled around briefly, and took flight. A few seconds later she landed near the nest again, poked her head into the entrance briefly, backed away, and flew off.

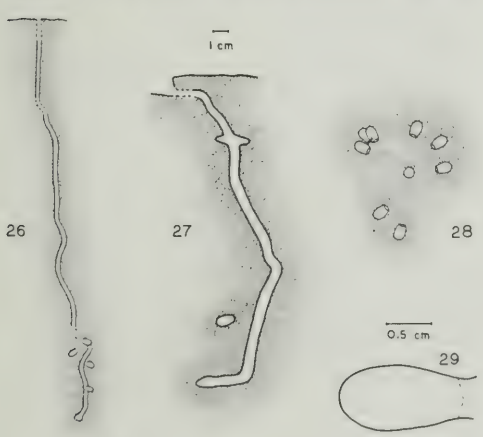
Andrena (*Holandrena*) *c. cressonii* Robertson

LaBerge (1986a) recently synonymized the subgenus *Opandrena* with *Holandrena* and recognized three subspecies of *Andrena* (*H.*) *cressonii.* One of these, *Andrena* (*H.*) *c. cressonii* is a common, polylectic, spring and early summer bee that ranges from the Atlantic coast westward to easternmost Texas, northeastern Kansas, most of Nebraska, and the eastern edges of Wyoming and Montana. North to south it extends from southernmost Canada to the Gulf coast (LaBerge 1986a). The observations presented here were made between 1980 and 1984.

Adult *Andrena cressonii* began to appear in the latter half of April in east-central Illinois. Early in the season, males patrolled vegetation (flowers, trees, and shrubs) in search of females, and it was there that mating frequently took place. On 1 May 1980, two mating pairs were observed on male catkins of *Salix interior* at a site near Rantoul, Illinois. In each case, the female rested quietly on the catkin with the male, in genital contact, curled upward and forward above her with his head over her abdomen. The male did not grasp the female with his legs, which he curled beneath his body. He made continuous, small amplitude, anterior-posterior, rocking movements and at intervals jerked the anterior part of his body downward toward the female three or four times in quick succession. The female was quite still except for slight abdominal pumping, but it was she who broke contact, appearing to brush at the male with her legs and flexing at the petiole. The first coupling lasted a minimum of 1 min 43 sec, the second at least 3 min 32 sec. On 25 and 26 April 1984, many male *A. cressonii* patrolled the abundant flower heads of dandelion (*Taraxacum officinale*) at Homer Lake. A male bee would fly slowly toward a flower head, hover near it briefly, and move on. Two mating pairs were seen on the flower heads.

Collections from *Salix* and other potential pollen/nectar sources at Homer Lake during 1983 and 1984 indicated that females were active at flowers for about eight weeks each year (Figure 2). Collections from 27 April through 22 June 1983 netted 241 females, including single specimens on the first and last days. During 1984, collections from 25 April through 29 June yielded 477 bees. The first two specimens were taken on 25 April, the last three on 18 June. Collection data indicated that males were active at flowers only about half as long as females. Fifty-six males were netted between 27 April and 22 June 1983. They were most abundant during the first two weeks of collections, and only one specimen was taken after 13 May. The trend was similar during 1984, when collections from 25 April to 29 June yielded 297 male bees. Abundant from 25 April to 6 May, only 15 were taken after the latter date. *Andrena cressonii*, therefore, appeared at flowers about the same time as *A. erythrogaster*, and the active seasons of males and females of both species were of similar lengths.

A single nest of *Andrena cressonii* was found near those of *A. erythrogaster* at Homer Lake in 1983. The bee was active on 20, 21, 22, and 23 May, when ten of her pollen-collecting trips were timed. They averaged 51 min 52 sec in duration (range: 28 min 5 sec–105 min 49 sec), and at least two pollen sources were used. Loads consisted of either bright yellow (possibly *Salix nigra*) or light yellow pollen, and the bee alternated between these two sources for the four pollen loads collected on 21 May. Average stay in the nest between foraging trips was 34 min 6 sec (N = 8; range: 14 min 59 sec–81 min).



FIGURES 26–29. Nest structure in *Andrena personata* and *A. cressonii*. Fig. 26. Nest of *A. personata*: vertical section of main burrow with positions of four cells shown. Fig. 27. Nest of *A. cressonii*: vertical section of main burrow and one cell. Fig. 28. Same nest as shown in Figure 27, horizontal plan showing arrangement of cells around main burrow. Fig. 29. Frontal section through a cell of *A. cressonii*.

The well-concealed nest entrance was located in the acute angle formed by two sides of a triangular depression that may have been a deer track. The first 2 cm of the main burrow were horizontal; the burrow then bent abruptly and proceeded downward at a steep angle (Figure 27). At a depth of 12.5 cm the burrow bent away from its previous course, became more nearly vertical, and proceeded to a depth of 20 cm, where it curved sharply toward the horizontal. It ran for a further 3 cm and ended in a rough-walled, slightly enlarged chamber, perhaps the beginning of a cell. Except for its initial 1 cm or so, the burrow was in good condition and open for its entire length. It was 4.5–5.0 mm in diameter to a depth of 4 cm, but expanded to 6–7 mm for the rest of its length. The burrow walls were roughened, but not as coarsely as those of *Andrena erythrogaster*. An interesting feature of the nest was four short (1 cm or less) branches off the main burrow at a depth of 4 cm. Three were roughly horizontal, the fourth inclined sharply upward, and all were narrower than the main burrow.

Eight cells were found in the nest at depths of 11.5–19.0 cm. Lateral burrows were tightly plugged with soil and shorter than those of *Andrena erythrogaster*; cells were only 2–4 cm from the main burrow (Figure 28). The long axis of the cell sloped at a shallow but distinct angle, the mouth of the cell higher than the rear. The angle of one cell was about 17°. Cells were ovoid in frontal section (Figure 29), although not always perfectly symmetrical. They were 12.5–13.4 mm long and 6.8–7.2 mm in maximum diameter, narrowing to a diameter of 4.3–4.5 mm at the closure. Cells of *Andrena cressonii*, therefore, were slightly smaller than those of *A. erythrogaster*. When the nest was excavated on 7 July, all cells contained post-defecating larvae, one of which was killed inadvertently. By 9 September, all larvae had pupated, and adults (five females, two males) emerged between 14 and 27 September.

Discussion

Andrena erythrogaster is the second member of the subgenus *Tylandrena* for which nesting biology has been studied in detail. Previously, Stephen (1966) reported on the bionomics of *A.* (*T.*) *perplexa* Smith (under the species name *A. viburnella*) from a site in Corvallis, Oregon; less complete observations were given by Parker and Böving (1924). Stephen (1966) found that several aspects of the biology of *A. perplexa* differed strikingly from what had been previously known for *Andrena*. Information on a second member of the subgenus, therefore, permits interesting comparisons. All further references to *A. perplexa* are from Stephen (1966) unless otherwise noted.

Three *Andrena perplexa* nesting sites were found in the central Willamette Valley of Oregon. Two, including Stephen's study site, were in lawns and the third was located in an area of native bunch grass. Because few bees nested in a barren driveway that intersected the study site, some degree of vegetative cover was thought to be prerequisite for nesting in this species. Rau's (1935) population of *A. erythrogaster* nested in grassy parts of his garden but also utilized the bare, hard-packed soil of footpaths. In the present study, *A. erythrogaster* nested in an area of dense vegetative cover (Homer Lake) and in ground where vegetation was sparser (Lodge Park). Some individuals dug nests beneath organic debris such as dead leaves.

Both species are to some degree gregarious and use the same nesting sites for a number of years. *Andrena perplexa* nests reached a density of 380 per square meter (Stephen 1966). Parker and Böving (1924) found its nests in great numbers alongside those of *Colletes rufithorax* Swenk in a sunny, south-facing slope on the grounds of Catholic University of America, Washington, D.C. Rau's perennial aggregation of *A. erythrogaster* varied in size from year to year (minimum about 20, maximum about 110); however, he gave no density figures. In the present study, collections showed *A. erythrogaster* to be abundant at both sites, but nesting aggregations were loose with nests generally well separated.

Emergence of males and females seems closely synchronized in both species. The sexes of *Andrena perplexa* appeared, at most, about a day apart, with males being slightly earlier. Rau (1935) indicated that male and female *A. erythrogaster* emerged together over a period of two or three days. Collections during the present study suggest that male *A. erythrogaster* can be found at host plants perhaps a day or two before females, but actual emergence times were not determined.

Stephen reported that male *Andrena perplexa* began patrolling the nesting site soon after emerging and that this activity continued for 10–12 days. Most matings occurred on the ground at the nesting site, but a few took place above ground on vegetation. He also reported several instances in which males followed females into their nests. Rau (1935) observed similar behavior among *A. erythrogaster*—males flying about the nesting site, resting in the grass, and entering burrows. He did not mention where mating took place. To this I can add little except that on several occasions males were observed flying about nonhost plants, such as maples, early in the season.

Among other *Andrena*, Johnson (1981) reported a similar range of male behavior in *A.* (*Melandrena*) *dunningi* Cockerell, and Barrows (1978) studied male behavior in *A. erigeniae* Robertson and summarized available data for other species.

Female *Andrena perplexa* spent the first two weeks of their adult lives engaged in nest construction. Although I obtained no direct data on the length of the preprovisioning period or the time required for nest construction in *A. erythrogaster*, collections from *Salix* spp. during 1983 and 1984 indicated that few of the females captured early in the season were collecting pollen and therefore had not yet begun provisioning. Perhaps they were constructing nests. The time required to excavate the main burrow and to construct the first cell must vary from species to species and among individuals according to such factors as nest depth, soil conditions, and weather. Since nests of *A. perplexa* averaged considerably deeper than those of *A. erythrogaster*, they probably took longer to excavate. Stephen found that *A. perplexa* females could dig 15–30 cm in an evening.

Nests of *Andrena erythronii* (Michener and Rettenmeyer 1956) averaged somewhat shallower (13.1 cm) than those of *A. erythrogaster*. During favorable weather, *A. erythronii* required about a day to excavate the main and lateral burrows and the first cell. If the digging abilities of *A. erythrogaster* are comparable, construction of the main burrow and initial cell should require slightly more time, perhaps a day or two under favorable conditions. Given the short period of adult activity of most solitary bees and the frequent inclement weather encountered by vernal species, selection probably favors traits for rapid excavation of nests and cells (without sacrificing progeny survival) that allow their bearers to take full advantage of favorable provisioning weather.

Various nest and cell characteristics differed markedly between the two species. The tumulus of *Andrena perplexa* was concentric, that of *A. erythrogaster* was eccentric; however, both lacked turrets, and entrances were unplugged except for short periods. Nests of *A. perplexa* reached 0.55–1.01 m in depth, two to three times as deep as those of *A. erythrogaster*. The main burrow of each species was nearly vertical, meandered little, and was excavated to its ultimate depth before construction of the first cell. Thereafter, *A. perplexa* tended to construct cells regressively, the depth of subsequent cells decreasing. *A. erythrogaster* exhibited a generally stationary pattern of cell construction, with most cells at about the same depth. Lateral burrows in *A. perplexa* were somewhat shorter (2–5 cm) than those of *A. erythrogaster* and were the same diameter as the main burrow. Distally, they bent abruptly downward and formed constricted necks before giving rise to single, vertical cells. The cells of *A. erythrogaster* were markedly sloping but far from vertical.

Few other *Andrena* have been reported to build vertical cells consistently. Schrader and LaBerge (1978), for example, found that the cells of *A.* (*Melandrena*) *regularis* Malloch were generally inclined at about 45°; those of the related *A.* (*M.*) *carlini* Cockerell ranged from vertical to nearly horizontal but were generally at about a 45° angle. Johnson's (1981) illustrations of the cells of *A. dunningi* indicated orien-

tations ranging from nearly horizontal to nearly vertical, and Thorp and Stage (1968) noted that the cells of *A.* (*Leucandrena*) *placida* Smith showed similar variability. The more common cell orientation in *Andrena* is nearly horizontal or slightly inclined, as has been reported for *A. erythronii* (Michener and Rettenmeyer 1956), *A. erigeniae* (Davis and LaBerge 1975), *A.* (*Thysandrena*) *candida* Smith (Youssef and Bohart 1968), *A. caerulea* Smith (Linsley and MacSwain 1959), and *A.* (*Callandrena*) *helianthi* Robertson (Parker and Bohart 1982).

The entire inner surfaces of the cells of *A. erythrogaster* and *A. perplexa* were lined with a waterproof secretion, as has been noted in other *Andrena*. Stephen described an additional inner lining around the basal two-fifths of cells of *A. perplexa*, a structure not detected in the cells of *A. erythrogaster*.

The provision masses of the two species differed markedly. That of *Andrena erythrogaster* was in the form of a moist, flattened sphere with considerable associated free nectar. In contrast, the bottom part of the mass of *A. perplexa* occupied the lower third or so of the cell, its shape determined by that of the cell. The top part of the mass, however, did not contact the cell walls and had been molded by the bee into a craterlike extension of the bottom part. The top surface was markedly concave and the egg had been inserted into it.

Johnson (1981) described the provision mass of *Andrena dunningi* as similar to that of *A. perplexa*, but his illustrations indicate that the entire mass had been molded by the bee, not merely the upper part. Schrader and LaBerge (1978) described the provision mass of *A. regularis* as "moist, subspherical, somewhat flattened . . . to which moisture had obviously been added." The mass of *A. regularis* shown in their figure 10 looks similar to that of *A. erythrogaster* except that it appears to have a more definite depression in the upper surface. Among other species in the genus, the most commonly reported shape for the pollen mass is nearly spherical, as in *A. erigeniae* (Davis and LaBerge 1975), or a spheroid depressed to some degree, as in *A.* (*Callandrena*) *accepta* Viereck (Rozen 1973).

Egg placement was similar in the two species. One end (probably the posterior) was inserted into the top of the provisions with the free end protruding at an angle above the mass. Schrader and LaBerge (1978) reported a similar egg placement for *A. regularis* and *A. carlini* as did Johnson (1981) for *A. dunningi*. Other variations in egg placement that have been reported for *Andrena* include eggs lying atop provision masses along more or less their full lengths, as in *A. erythronii* (Michener and Rettenmeyer 1956) and eggs with both ends in contact with the mass but the midportion free, as in *A. candida* (Thorp and Stage 1968).

Many factors influence the reproductive success of solitary bees, including a diverse group of predators, parasites, and pathogens. For vernal species such as *Andrena erythrogaster*, however, environmental adversities, particularly cool, wet weather, may be of greater importance. Inclement weather affects the entire population, slowing or halting foraging activity for hours or days and reducing the time available to these short-lived insects for rearing young. Year-to-year variation in the number of cells per nest was noted for *A. erythrogaster* during the present study and may have been due in part to yearly differences in the number of days of suitable foraging weather. Rau (1935) felt that the amount of rainfall during the nesting season was the most important factor controlling the size of his population of *A. erythrogaster*, and Stephen (1966) also discussed the effects of adverse weather on the activities of *A. perplexa*. He noted that when bad weather prevented females from foraging for one or more days, they tended to begin flight activities on the following day at lower than normal temperatures. Since many studies of the biology of solitary bees are short term or opportunistic in scope, the complex relationship between the bee and its environment is dealt with superficially if at all. Longer-term studies emphasizing this aspect of a bee's life history should prove enlightening.

Although the genus *Andrena* includes several hundred North American species, many people are unaware of the importance of these bees as pollinators of wild flowering plants and certain commercial crops (blueberries, for example; Boulanger et al. 1967). Our knowledge of such aspects of *Andrena* biology as nesting, mating, and foraging behavior and the ecological role these common bees play is, however, slowly expanding. As this and other studies show, behavioral traits vary from species to species, sometimes in subtle ways, just as interspecific morphological variation is at times slight.

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